



Revealing stock–recruitment relationships in lobsters and crabs: is experimental ecology the key?

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Abstract

As is true for many fish and invertebrate fisheries, stock–recruitment relationships remain poorly understood for most commercially important species of lobsters and crabs. This paper gives a critical overview of advances in assessing the relative importance of pre- and post-settlement processes to the recruitment of 14 commercially and/or ecologically important lobsters and crabs. Three case studies (western rock lobster, *Panulirus cygnus*, blue crab, *Callinectes sapidus*, and the American lobster, *Homarus americanus*) are used to illustrate where standard fishery survey methods, combined with field experiments, have provided insights into the form of stock–recruit relationships and the ecological processes that influence them. It is notable that larval supply-dominated cases, such as that of *P. cygnus*, may be less common than those dominated by post-settlement processes, such as *C. sapidus*, in which strong compensatory processes lead to non-linear spawner-to-recruit or juvenile-to-recruit relationships. In other cases, such as *H. americanus*, the influence of post-settlement controls remains controversial. Significant settler or juvenile-to-recruit linkages have been reported more often than spawner-to-recruit relationships, most likely because pre-settlement processes often mask the latter. Innovative field experiments, early life stage monitoring and spatial modeling have improved our understanding of the influence of competition, predation, cannibalism, sociality and movements to the demography of some of these species. Field experiments have been more widely used by American and Australian than European investigators. Ecological experiments are not a panacea, though, and can lead to misinterpretation, especially of the relative importance of mortality and emigration. Uncertainties about age and the relevant spatial scale at which to evaluate stock–recruitment relationships have posed further challenges. This review underscores the need to design ecological studies at a geographic scale that will better reveal the stock–recruitment relationship.

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Keywords: Recruitment; Density-dependence; Mortality; Dispersal; Decapod; Experimental ecology

1. Introduction

In marine species with complex life histories, involving larval dispersal and settlement to the seabed, a host of physical and biotic processes influence the fate of a cohort, both before and after settlement. It is convenient to divide these processes into two parts: (1) *pre-settlement* processes, operating

from the time of hatching to initial larval settlement, and (2) *post-settlement* processes, operating for the remainder of benthic life from early juvenile stages through adulthood. All commercially exploited marine decapod crustaceans, such as lobsters, crabs and shrimps have complex life histories. However, differences in life history traits such as age and size at maturity, fecundity, larval duration and dispersal can dramatically influence a species' ecological success and resilience to harvesting.

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Much of the focus of fisheries stock assessment is on determining the extent to which the reproductive potential of the adult population is realized as subsequent recruitment to the next generation. Evaluating this so-called stock (or spawner)-to-recruit relationship (SRR) for most species of crabs and lobsters has remained an elusive goal. In an earlier review of decapod fisheries, Cobb and Caddy (1989) remarked that, “There is little information on the spawner–recruitment relationship, but understanding it may lead to a better understanding of the underlying dynamics of the population”. They further proposed that “The next major step forward in understanding decapod population dynamics will come from experimental manipulation in the field”.

Over the past two decades, much ecological research on crabs and lobsters has focused on determining the relative importance of pre- and post-settlement processes to recruitment (e.g., Caputi and Brown, 1993; Eggleston and Armstrong, 1995; Pile et al., 1996; Wahle and Incze, 1997). For commercially exploited species this work has augmented traditional fishery survey methods with methodology and theory developed with non-commercial species that tend to be more experimentally tractable (e.g., Roughgarden et al., 1988; Underwood, 1997). The net result has been to improve stock assessment methods and obtain a better mechanistic understanding of recruitment processes. Now, more than a decade since Cobb and Caddy’s review, it is helpful to take a critical look at the contribution of experimental ecology to our understanding of decapod population dynamics.

This paper presents a review of the literature on 14 species of crabs and lobsters: five spiny lobsters, three clawed lobsters, and six brachyuran and anomuran crabs. The first section provides an overview of (1) spawner-to-recruit and juvenile-to-recruit relationships reported for these species, (2) the application of experimental ecological approaches and (3) the ecological processes inferred from these studies. The second section profiles three case studies, two of which illustrate opposite extremes in the dominance of pre- and post-settlement processes to adult recruitment. The third is a more controversial case that likely falls somewhere in between. Along the way, experimental approaches that have been particularly illuminating to our understanding of recruitment processes are highlighted. Equally, areas where experimental meth-

ods have fallen short or have been misleading are emphasized. The concluding section identifies major voids in knowledge and outlines possible directions for future research.

The species reviewed represent a cross-section of commercially important, and relatively well studied, crabs and lobsters around the world. One of them is only lightly exploited (*Carcinus maenas*), but is included because it has been the subject of extensive experimental work on pre- and post-settlement processes. The literature search was conducted using Aquatic Sciences and Fisheries Abstracts bibliographic database from 1982 to 2001. In this paper, the term recruitment is used in its general sense as the number of individuals surviving to a particular age, size or life stage. Where I refer to recruitment to harvestable size it is made explicit.

1.1. Fisheries versus ecological approaches

At the outset it is necessary to be clear about the differences in scientific perspectives of fisheries science and marine ecological literature. Much marine ecological literature over the past two decades has focused on assessing the relative importance of pre- and post-settlement processes in determining demographic patterns. Experimentally tractable taxa such as barnacles (e.g., Roughgarden et al., 1988), colonial invertebrates (e.g., Hughes, 1990) and reef fishes (e.g., Doherty and Fowler, 1994) with widely dispersed larvae, but sessile or sedentary adults, have provided insights into the role of larval supply and dispersal on patterns of adult populations. The recognition of “supply side ecology” as a major determinant of demographic patterns has helped broaden the context in which marine ecologists view benthic populations and communities (reviewed by Caley et al., 1996). Post-settlement processes such as competition, predation and disturbance, which had previously been the focus of investigation (e.g., Paine, 1974; Sousa, 1980; Connell, 1983), could now be viewed in the context of larval supply (e.g., Raimondi, 1990; Schmitt and Holbrook, 1999). Two major advances resulted. First, there was explicit recognition that most studies were conducted at such a small spatial scale that the larval settlement and recruitment to local populations was decoupled from the reproductive performance of resident adults and were largely dependent on larval

delivery processes (Roughgarden et al., 1988). This view acknowledged the existence of the metapopulation: an aggregate of open subpopulations interconnected in marine species mostly by larval dispersal (Hanski and Gilpin, 1997). Second, the long-standing ecological debate over whether marine populations were resource limited could now be recast in more spatial terms as a question of the status of local, open populations on a continuum of density-dependent and independent controls varying in space and time (e.g., Raimondi, 1990; Forrester, 1995). However, as field studies have generally been conducted at the level of the local population and rates of exchange between these populations are still poorly understood, Caley et al. (1996) remarked, that “linking empirical studies with population dynamics theory can still only be done at a relatively small spatial scale”.

By comparison, fisheries science has had a longer history of recognizing the importance of larval supply in determining cohort success (Hjort, 1914; Sinclair, 1988). In fact, much of the focus of traditional fishery stock assessment has been to evaluate the relationship between spawning stock or juvenile abundance and subsequent recruitment to harvestable stages in order to assess the degree of density-dependent regulation, i.e., the extent to which per capita survival or reproductive yield depend on population size (Ricker, 1954; Beverton and Holt, 1957; Cushing and Harris, 1973, reviewed by Fogarty et al., 1991; Myers et al., 1995). Due to a largely correlative approach, however, the fisheries literature has often lacked a mechanistic understanding of cause–effect linkages influencing recruitment. Although fishery stock assessment surveys may be conducted at large spatial scales to determine the relationship between spawning stock and subsequent recruitment to the fishery, standard fishery surveys often miss the early life stages. Furthermore, political boundaries often preclude a comprehensive assessment of a population. On limited budgets, efforts to elucidate causal mechanisms from either direct observations or experiments have been relatively rare. It has been argued that experimental approaches can help evaluate complex relationships often confounded in fishery survey data (Peterson, 1990), but neither large-scale fishery surveys nor small-scale ecological experiments have yet provided an adequate understanding of the causes and demographic consequences of population exchange, via planktonic or

benthic dispersal. At present, few examples exist in which the consequences of population exchange for resilience and sustainability have been evaluated, even theoretically for decapods (e.g., Botsford et al., 1998; Fogarty, 1998; Stockhausen et al., 2000). It is therefore worthwhile to assess how experimental ecological methods, combined with fishery survey approaches, have advanced our understanding of the demography of large-bodied crustaceans.

2. Overviews

2.1. Spawner-to-recruit and juvenile-to-recruit relationships

Evidence for density-dependent population regulation has traditionally been sought by evaluating either spawner-to-recruit or juvenile-to-recruit relationships (Fig. 1a). In stock assessment, it is conventional to fit negative density-dependent models such as compensatory and over-compensatory functions (Fig. 1b; Beverton and Holt, 1957; Ricker, 1954, respectively). Simple power or linear functions are also employed in cases that exhibit weak or non-existent density effects, respectively (Hilborn and Walters, 1992). In the literature reviewed in this paper, a full range of density-independent to dependent relationships were found for large decapods.

Among the 13 commercially exploited species reviewed, there were only four species with unchallenged spawner–recruit relationships (Table 1a and b): the blue crab (*C. sapidus*), tanner crab (*Chionoecetes bairdi*), king crab (*Paralithodes camtschaticus*), and western rock lobster (*P. cygnus*). In the first three cases the relationship was found to be either compensatory or over-compensatory. In the case of *P. cygnus*, though, early indications of a strong over-compensatory spawner–recruit relationship (Morgan et al., 1982) were not borne out by later research (see case 1). Over much of this species' range there is no significant spawner–recruit relationship, except in one offshore archipelago of Western Australia where the spawning stock was especially depleted (Caputi et al., 1995a). In this case, as well as for blue crab in Chesapeake Bay (Uphoff, 1998), the spawner–recruit relationship was enhanced if environmental factors, presumed to affect larval supply,

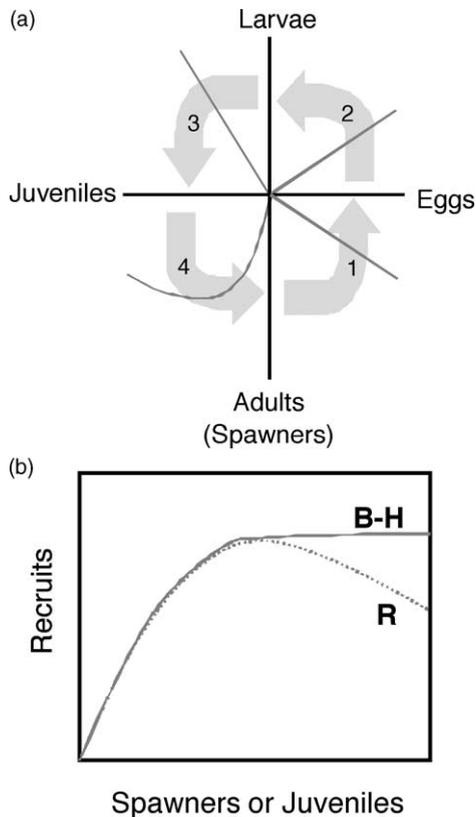


Fig. 1. (a) Pawlik diagram illustrating the difference between spawner-to-recruit and juvenile-to-recruit relationships. If recruitment is defined as the number of individuals entering the adult (spawner) stage, for example, then the spawner–recruit relationship is the quantitative link between adults and their offspring as adults (follow the arrows from quadrants 1 to 4 in the diagram). The juvenile–recruit relationship is the link between juveniles and adults of the same cohort (quadrant 4). (b) The form of two models conventionally used to describe and evaluate density-dependent spawner or juvenile-to-recruit relationships: the Beverton–Holt model (B–H) is an asymptotic, compensatory, function; the Ricker model (R) is dome shaped and over-compensatory.

were included in the regression (Table 1). On the other hand, a compensatory spawner–recruit relationship reported for the American lobster by Ennis and Fogarty (1997) remains “tenuous”, to quote the authors, because of uncertainty of size at age and the source of larvae.

Key environmental factors alone satisfactorily predict postlarval settlement, if not catch, in several cases (Table 1). This presumably reflects the overriding influence the physical environment can have on larval

delivery, survival and subsequent recruitment. For 6 of the 13 commercial species surveyed, postlarval settlement or fishery recruitment trends were successfully predicted from environmental variables including temperature, rainfall, net along-shore transport, winds and sea level (an index of El Niño Southern Oscillation). Drinkwater et al. (1996) noted, however, that American lobster catches correlated well with temperature anomalies up to the mid-1980s, but did not predict a more recent population boom (see case 3).

Even greater success has been achieved with juvenile-to-recruit relationships (Table 1). Eight of the 13 commercially exploited species in this survey were reported to have significant juvenile-to-fishery recruit relationships. The western rock lobster, *P. cygnus*, is perhaps the most famous example in which a settler-to-recruit relationship is used as a forecasting and management tool (Caputi et al., 1995b,c, 1998, see case 1). Significant settler or early juvenile-to-fishery recruit relationships have also been reported for the Caribbean spiny lobster *Panulirus argus* (only in Cuba), blue crab, *C. sapidus*, tanner crab, *C. bairdi*, and Norway lobster, *Nephrops norvegicus* (Table 1a). For several species, settler-to-fishery recruit relationships have not yet been established, but the demonstration of significant settler-to-older juvenile relationships or a geographical correspondence between settlement “hot spots” and strong harvest areas may bode well for harvest forecasting in the future (e.g., New Zealand rock lobster, *Jasus edwardsii* (Breen and Booth, 1989; Booth et al., 2001); American lobster, *H. americanus* (Incze and Wahle, 1991; Incze et al., 1997; Miller, 1997; Steneck and Wilson, 2001)).

The strength of density-dependent controls varies by species, and even regionally within species. For example, there was evidence of strong density-dependence for the blue crab, *C. sapidus* in Delaware Bay where an over-compensatory young-of-year-to-fishery recruit relationship was reported (Kahn et al., 1998). A somewhat weaker, compensatory (Beverton–Holt) relationship was found for blue crabs in Chesapeake Bay (Lipcius and Stockhausen, 2002). For *H. americanus* a compensatory relationship was reported between planktonic postlarval abundance and subsequent stock size (Fogarty and Idoine, 1986), although there is some debate over the validity of this relationship (see case 3). Nearly linear power functions described for *P. cygnus* reflect an even weaker

Table 1
Reported spawner-to-recruit, spawner and/or environment-to-recruit, and juvenile-to-recruit relationships for the (a) lobsters and (b) crabs surveyed in this review^a

Species	Location	Spawner-to-recruit			Spawner and/or environment-to-recruit			Juvenile-to-recruit		
		Source	Function	x/y variables	Source	Function	x/y variables	Source	Function	x/y variables
(a) Lobsters										
Spiny lobsters										
<i>P. cygnus</i>	W Australia	Morgan et al. (1982) ^b	Ricker	Spawning stock/postlarval index	Caputi et al. (1995a)	Power	Spawner catch rates, sea level, rainfall/postlarval	Morgan et al. (1982) ^b	Ricker	Postlarval index/juvenile catch, spawning stock
		Caputi et al. (1995a)	Power	Spawning stock/postlarval index	Caputi et al. (1998)	Power	Spawner catch rates, sea level, rainfall/postlarval	Caputi et al. (1995b)	Power	Postlarval index, juvenile catch/commercial catch
								Caputi et al. (1995c)	Power	Postlarval index, juvenile catch/commercial catch
<i>P. argus</i>	Bahamas	–	–	–	Eggleston et al. (1998a)	Linear	Wind, lunar periodicity/postlarval settlement	–	–	–
	Florida	–	–	–	–	–	–	Forcucci et al. (1994)	Linear	Postlarval settlement/juveniles
	Cuba	–	–	–	–	–	–	Cruz et al. (1995)	Linear	Juvenile index/commercial catch
<i>P. marginatus</i>	Hawaii	–	–	–	Polovina and Mitchum (1994)	Linear	Sea level/catch	–	–	–
<i>J. edwardsii</i>	New Zealand	–	–	–	–	–	–	Breen and Booth (1989)	Linear	Postlarval index/age 1+, 2+, 3+
								Booth et al. (2001)	Linear	Postlarval index/age 1+, 2+, 3+
Clawed lobsters										
<i>H. americanus</i>	NE US, Canada	Ennis and Fogarty (1997) ^b	Beverton–Holt	Egg production/fishery recruitment	Drinkwater et al. (1996)	Linear	Temperature/landings	Fogarty and Idoine (1986) ^b	Beverton–Holt	Planktonic
								Incze and Wahle (1991)	Linear	Planktonic postlarvae/juvenile
								Incze et al. (1997)	Linear	Planktonic postlarvae/juvenile

Table 1 (Continued)

Species	Location	Spawner-to-recruit			Spawner and/or environment-to-recruit			Juvenile-to-recruit		
		Source	Function	<i>x/y</i> variables	Source	Function	<i>x/y</i> variables	Source	Function	<i>x/y</i> variables
								Miller (1997)	Linear spatial correlation	Planktonic postlarvae/ exploitable stock
								Steneck and Wilson (2001)	Linear spatial correlations	Juvenile/commercial catch
<i>H. gammarus</i>	Europe	–	–	–	–	–	–	–	–	–
<i>N. norvegicus</i>	Europe	–	–	–	–	–	–	Nichols et al. (1987)	Linear-note inverse relationship	Larval production/parental female stock
(b) Crabs										
<i>C. magister</i>	NW US, Canada	–	–	–	McConnaughey et al. (1992)	None given (inverse)	Net along-shore transport/ young-of year index	Eggleston and Armstrong (1995)	Linear	Postlarval settlement/early juveniles
					McConnaughey et al. (1994)	None given (inverse)	Net along-shore transport/commercial catch			
<i>C. pagurus</i>	North Europe	–	–	–	–	–	–	–	–	–
<i>C. sapidus</i>	Eastern US	Lipcius and Van Engle (1990)	Ricker	Spawner/fishery recruitment	Uphoff (1998)	Ricker	Spawner stock, water temp/recruit index	Olmi et al. (1990)	Linear	Planktonic postlarvae/juvenile abundance
		Kahn et al. (1998)	Ricker	Spawner/fishery recruitment				Pile et al. (1996)	Linear and non-linear	Early/late juvenile stages
		Lipcius and Stockhausen (2002)	Beverton–Holt, Power	Spawner/larvae, postlarvae				Kahn et al. (1998)	Ricker	Young-of-year/fishery recruits, “large” crabs
								Lipcius and Stockhausen (2002)	Linear	Larvae/postlarvae
<i>C. maenas</i>	North Europe	–	–	–	–	–	–	–	–	–
<i>C. opilio</i>	E Canada, Alaska	–	–	–	–	–	–	Moriyasu et al. (1998)	Linear	Post-season trawl catch/legal catch the next year

<i>C. bairdi</i>	Alaska	Zheng and Kruse (1998, 1999)	Ricker	Spawning biomass/fishery recruitment	Rosenkranz et al. (1998)	Linear	May–June NE winds/fishery recruitment	Hilsinger (1982)	Linear	Pre-recruit catch/legal catch
<i>P. camtschaticus</i>	Alaska	Zheng et al. (1995)	Ricker	Spawning biomass/fishery recruitment	–	–	–	–	–	–

^a Tenuous or not borne out by subsequent research.

^b Independent and dependent variables in the relationship tabulated as x/y . Recruits defined in the broad sense as individuals reaching a later stage of development (y) from an earlier stage (x).

compensatory relationship. Evaluating relationships between finer subdivisions of age can reveal the timing of onset of density-dependent processes in the life history (e.g., Hilsinger, 1982; Breen and Booth, 1989; Incze and Wahle, 1991; Eggleston and Armstrong, 1995; Pile et al., 1996; Incze et al., 1997; Wahle and Incze, 1997; Moriyasu et al., 1998; Moksnes et al., 1998).

These findings bear out Cobb and Caddy's (1989) observation that environmental "noise" often overwhelms the spawner–recruit signal in crabs and lobsters (e.g., Caputi et al., 1995a). As in other species with complex life cycles, spawner–recruit relationships exist in theory (Hilborn and Walters, 1992), but the difficulty in resolving the relationship stems from the fact that (1) the spawner–recruit relationship involves two generations: the parents and resultant offspring at some benthic stage, and (2) biological and physical factors operating between spawning and recruitment can confound a clear functional relationship.

2.2. Experimental approaches

Tables 2 and 3 list the range of experimental and other methodologies relevant to recruitment studies of the 14 decapod species surveyed. Experimental interventions (Table 2) fall into five major categories: population manipulations, resource manipulations, predator inclusion/exclusion experiments, tethering experiments, and mark-recapture experiments. Table 3 lists other investigative approaches that have been helpful in understanding post-settlement dynamics: (1) collectors for larval and postlarval settlement stages; (2) benthic sampling methods for post-settlement stages other than commercial traps; (3) novel methods in age determination; (4) gut content analysis of predators.

Population addition or removal experiments with crabs and lobsters have been conducted in most cases to assess the efficacy of population enhancement (Bannister et al., 1994; Bannister and Addison, 1998; Van der Meeren, 2000), evaluate early post-settlement survival or determine inter- and intra-cohort effects on growth and survival (Ford et al., 1988; Eggleston and Lipcius, 1992; Butler and Herrnkind, 1997; Iribarne et al., 1994; Fernandez, 1999; Wahle and Incze, 1997; Wahle et al., 2001). One case listed in this category involved the comparison of no-fish con-

servation areas with fished reference areas (DeMartini et al., 1993). Although population manipulations have illuminated factors influencing post-settlement mortality and movements, several questions often arise: (1) Are sufficient unmanipulated control treatments included in the experimental design? (2) Are the manipulated densities realistic? (3) Does the manipulation introduce unintended artifacts and can they be accounted for? (4) Do hatchery or lab-reared individuals behave the same as wild stock?

Resource manipulation experiments (e.g., shelter, habitat or food additions or removals) have been conducted widely with crabs and lobsters to assess the impact of changes in a resource on local population densities, either by larval settlement, immigration or survival (Table 2). Few studies have examined the joint effects of food and habitat (Marx and Herrnkind, 1985), probably because habitat was judged to have an overriding influence on lobster and crab distributions. Habitat manipulation experiments have examined the spatial configuration, size, shape and connectivity of habitat patches in the benthic environment (*P. argus*—Eggleston and Lipcius, 1992; Lipcius et al., 1998; *H. americanus*—Bologna and Steneck, 1993; *C. sapidus*—Eggleston et al., 1998b; Michaeli and Peterson, 1999; Hovel and Lipcius, 2001). Habitat scaling is particularly important to evaluate because of the non-linear effects of habitat area and structural complexity on population density or survival (Eggleston et al., 1998b; Lipcius et al., 1998; Hovel and Lipcius, 2001). For recruitment studies at any scale, it is important to determine whether habitat enhancements (including artificial reefs) augment recruitment or simply cause a concentration of individuals (Bohnsack, 1989; Castro et al., 2001).

Predator exclusion or inclusion experiments have been employed to distinguish losses related to predation (both inter- and intra-specific) from emigration losses (Table 2; especially Eggleston and Lipcius, 1992; Iribarne et al., 1994; Eggleston and Armstrong, 1995). A latent difficulty with these types of experiments relates to potential artifacts of the enclosure on the behavior of both predator and prey that could alter prey densities and measured survival rates. In these experiments, the challenge is to design the enclosure in such a way as to minimize these artifacts and run parallel control treatments that mimic the experimental treatment in all ways except the predator treatment.

Table 2

Experimental methodologies related to settlement and post-settlement processes for the crab and lobster species surveyed in this review

Species	Location	Methodology				
		Population manipulation	Resource manipulation	Enclosure/exclosure	Tethering	Mark-recapture
Spiny lobsters						
<i>P. cygnus</i>	W Australia	Ford et al. (1988)	–	–	–	Chittleborough and Phillips (1975), Ford et al. (1988)
<i>P. argus</i>	Florida, Bahamas, Mexico, Cuba	Eggleston and Lipcius (1992), Butler and Herrnkind (1997)	Marx and Herrnkind (1985), Eggleston et al. (1990, 1992), Eggleston and Lipcius (1992), Mintz et al. (1994), Butler and Herrnkind (1997), Herrnkind et al. (1997), Sosa-Cordero et al. (1998)	Eggleston and Lipcius (1992)	Herrnkind and Butler (1986), Smith and Herrnkind (1992), Eggleston et al. (1992), Mintz et al. (1994), Acosta and Butler (1997), Lipcius et al. (1998), Acosta and Butler (1999)	Forcucci et al. (1994), Butler and Herrnkind (1997), Butler et al. (1997), Acosta (1999)
<i>P. marginatus</i>	Hawaii	DeMartini et al. (1993) ^a	–	–	–	–
<i>J. edwardsii</i>	New Zealand	–	Butler et al. (1999)	–	Butler et al. (1999)	–
Clawed lobsters						
<i>H. americanus</i>	East US, Canada	Wahle and Incze (1997), Wahle et al. (2001)	Bologna and Steneck (1993), Wahle and Incze (1997), Palma et al. (1998), Castro et al. (2001)	Lavalli and Barshaw (1985), Barshaw and Lavalli (1988), Wahle et al. (2001)	Wahle and Steneck (1992), Barshaw and Able (1990)	Krouse (1981), Robichaud and Cambell (1995), Wahle and Incze (1997), Cowan (1999), Comeau et al. (1999)
<i>H. gammarus</i>	Northern Europe	Bannister et al. (1994), Bannister and Addison (1998), Van der Meeren (2000)	Robinson and Tully (2000), Linnane et al. (2000)	–	–	Bannister et al. (1994), Bannister and Addison (1998)
<i>N. norvegicus</i>	Northern Europe	–	–	–	–	Bailey (1986)
Crabs						
<i>C. magister</i>	NW US, Canada	Iribarne et al. (1994), Fernandez (1999)	Fernandez et al. (1993a), Iribarne et al. (1994), Eggleston and Armstrong (1995), Fernandez (1999), Morgan et al. (1996)	Iribarne et al. (1994), Eggleston and Armstrong (1995), Fernandez (1999)	Fernandez et al. (1993b)	–

Table 2 (Continued)

Species	Location	Methodology				
		Population manipulation	Resource manipulation	Enclosure/exclosure	Tethering	Mark-recapture
<i>C. pagurus</i>	North Europe	–	–	–	–	Bell et al. (2003)
<i>C. sapidus</i>	East US, Gulf of Mexico	–	Moksnes et al. (1997), Morgan et al. (1996), Eggleston et al. (1998b), Blackmon and Eggleston (2001)	–	Hines and Ruiz (1995), Pile et al. (1996)	Fitz and Wiegert (1992), Blackmon and Eggleston (2001), Etherington et al. (2003)
<i>C. maenas</i>	North Europe	–	Hedvall et al. (1998), Moksnes and Wennhage (2001)	–	Dumas and Witman (1993), Moksnes et al. (1998)	Munch-Petersen et al. (1982)
<i>C. opilio</i>	E Canada, Alaska	–	–	–	–	–
<i>C. bairdi</i>	Alaska	–	–	–	–	–
<i>Paralithodes</i>	Alaska	–	–	–	–	–

^a No-fish conservation area.

Table 3

Additional methodologies providing insight into settlement and post-settlement processes for the crab and lobster species surveyed in this review

Species	Location	Methodologies			
		Larval, postlarval collectors	Dive, trawl, suction sampling	Aging methods	Gut analysis
Spiny lobsters					
<i>P. cygnus</i>	W Australia	Phillips (1972)	Jernakoff et al. (1994)	Sheehy et al. (1998)	Howard (1988)
<i>P. argus</i>	Florida, Bahamas, Mexico, Cuba	Cruz et al. (1995), Herrnkind and Butler (1994), Forcucci et al. (1994), Lipcius et al. (1997), Eggleston et al. (1998c), Stockhausen et al. (2000)	Herrnkind and Butler (1994), Field and Butler (1994), Forcucci et al. (1994), Butler et al. (1995), Lipcius et al. (1997), Childress and Herrnkind (1997), Herrnkind et al. (1997), Acosta and Butler (1997), Butler et al. (1997), Acosta (1999)	–	–
<i>P. marginatus</i>	Hawaii	–	Parrish and Polovina (1994), Polovina et al. (1995)	–	–
<i>J. edwardsii</i>	New Zealand	Booth and Tarring (1986), Breen and Booth (1989), Booth et al. (2000, 2001)	Breen and Booth (1989), Booth et al. (2000, 2001)	–	–
Clawed lobsters					
<i>H. americanus</i>	East US, Canada	Incze et al. (1997), Palma et al. (1998, 1999)	Hudon (1987), Able et al. (1988), Wahle and Steneck (1991), Lawton and Lavalli (1995) (review), Palma et al. (1998)	Wahle et al. (1996)	Hanson and Lanteigne (2000)
<i>H. gammarus</i>	Northern Europe	–	Howard (1980), Robinson and Tully (2000)	Sheehy et al. (1996, 1999)	–
<i>N. norvegicus</i>	Northern Europe	–	Gonzalez-Gurriaran (1987), Bailey (1986), Maynou et al. (1996)	Hillis and Tully (1993a), Belchier et al. (1994)	Armstrong et al. (1991)
Crabs					
<i>C. magister</i>	NW US, Canada	Fernandez et al. (1993a), Eggleston and Armstrong (1995), Eggleston et al. (1998c)	–	–	–
<i>C. pagurus</i>	North Europe	–	Robinson and Tully (2000)	–	–
<i>C. sapidus</i>	East US, Gulf of Mexico	Van Montfrans et al. (1995), Morgan et al. (1996), Eggleston et al. (1998b), Guillory et al. (1998)	Pile et al. (1996), Pardieck et al. (1999), Etherington and Eggleston (2000)	Ju et al. (2001)	–

Table 3 (Continued)

Species	Location	Methodologies			
		Larval, postlarval collectors	Dive, trawl, suction sampling	Aging methods	Gut analysis
<i>C. maenas</i>	North Europe	Moksnes and Wennhage (2001)	Moksnes and Wennhage (2001)	–	–
<i>C. opilio</i>	E Canada, Alaska	–	Lovrich et al. (1995), Sainte-Marie et al. (1996), Comeau et al. (1998), Moriyasu et al. (1998)	–	Jewett (1982), Waiwood and Elner (1982), Robichaud et al. (1986, 1991), Livingston (1989), Lilly (1991), Lovrich et al. (1995) Livingston (1989)
<i>C. bairdi</i>	Alaska	–	–	–	Livingston (1989)
<i>Paralithodes camtschatica</i>	Alaska	Blau and Byersdorfer (1994)	–	–	Livingston (1989)

Tethering has been widely used in predation studies to assess how relative predation rates vary with prey body size, habitat quality and location (Table 2). The most rigorous tethering experiments include video monitoring or controls for artifacts of the experimental manipulation, and give some assurance that the recognized artifacts of tethering do not interact with the experimental treatment effect (see Peterson and Black (1994) for discussion). It is important to recognize that tethering experiments provide a relative measure of predation “potential”, not necessarily a measure of absolute predation rates. In some cases, predation rates may also be inferred from gut content analysis of the predators (Table 3, Livingston, 1989; Armstrong et al., 1991; Lilly, 1991; Robichaud et al., 1991; Hanson and Lanteigne, 2000).

Mark-recapture experiments have been traditionally used with decapods to assess movement and growth (Table 2), but have been applied more frequently over the past decade to assess population size and dynamics (Table 2, especially Fitz and Wiegert, 1992; Forcucci et al., 1994; Bell et al., 2003). Most recently, an effort has been made to separate losses into mortality and emigration components (Etherington et al., 2003). Often the greatest challenge in applying mark-recapture methods for population studies is in satisfying sometimes restrictive assumptions regarding movements out of the study area, catchability, tag loss and mortality and behavior artifacts related to tagging (for discussions see Phillips (1990), Bannister et al. (1994), Etherington et al. (2003) and Bell et al. (2003)).

As for sampling and survey methodologies, over the past two decades there has been much experimentation with various types of passive larval and postlarval collectors in the development of abundance indices for early life stages (Table 3). Various types of plastic meshes and other artificial materials are effective at attracting settlers (e.g., Phillips, 1972; Palma et al., 1998; Blau and Byersdorfer, 1994; Booth and Tarring, 1986; Cruz et al., 1995; Van Montfrans et al., 1995). In other cases, natural substrates placed in deployable–retrievable units are equally or more effective (Eggleston and Armstrong, 1995; Incze et al., 1997; Moksnes and Wennhage, 2001). Sometimes, however, the most cost effective strategy is to apply a standardized sampling method in the naturally occurring settlement habitat (Wahle and Steneck, 1991; Pile

et al., 1996; Incze et al., 1997). More detailed discussion of the variety of trawl, diver visual survey and suction sampling methodology is beyond the scope of this review, but references are listed in Table 3.

Age determination is a challenge specific to crustaceans. Having an accurate and reliable indicator of age would remove the uncertainty of identifying age classes in crab and lobster populations. Body size may be an adequate proxy for age where individuals grow quickly and cohorts remain in distinct size groups (e.g., *Panulirus*). For slower growing species (e.g., *Homarus*) resolving age groups by size becomes confounded by heritable and environmental effects on growth (Nelson et al., 1980; Pollock, 1993; Sheehy, 2001; Wahle et al., 2001). The “age pigment”, lipofuscin, occurring in crustacean brain tissue, has been explored with some success as an alternative aging tool in several decapods (Table 3), but the method must be used judiciously as there remain questions about environmental effects on this indicator (Sheehy et al., 1999; Wahle et al., 2001; Ju et al., 2001).

2.3. Ecological processes

Post-settlement processes operating on the 14 decapods reviewed have been inferred from experiments and population surveys and are listed in Table 4. Table 5 identifies cases in which mortality, growth and/or movements have been explicitly shown to be density-dependent. Predation on early benthic stages is perhaps the process most widely inferred to influence the demography of these crabs and lobsters. Fishes, brachyuran crabs and octopi were most often cited as predators of juvenile stages. Evidence of predation stems from direct observation, gut content analysis of predators, tethering experiments and predator exclusion experiments (Tables 2 and 3). A consistent theme is that small-bodied early life stages tend to be associated with the protection afforded by structurally complex habitats, and emerge from those habitats as they outgrow vulnerability to predation.

Reports of cannibalism were exclusively found among the crabs surveyed (Table 4). Inter-cohort cannibalism in blue crab, *C. sapidus* (Hines and Ruiz, 1995), Dungeness crab, *Cancer magister* (e.g., Fernandez et al., 1993a,b), and snow crab, *Chionoecetes opilio* (Lovrich and Sainte-Marie, 1997), has been invoked as a possible explanation for

Table 4

References in the literature to post-settlement processes inferred to be operating in the crab and lobster species surveyed in this review

Species	Location	Post-settlement process					
		Interspecific predation	Cannibalism	Habitat or shelter limitation	Food limitation	Disease/algal toxins	Sociality
Spiny lobsters							
<i>P. cygnus</i>	W Australia	Howard (1988)	–	–	–	–	–
<i>P. argus</i>	Florida, Bahamas, Belize	Herrnkind and Butler (1986), Eggleston et al. (1990), Smith and Herrnkind (1992), Eggleston et al. (1992), Eggleston and Lipcius (1992), Mintz et al. (1994), Acosta and Butler (1997), Butler et al. (1997)	–	Marx and Herrnkind (1985), Eggleston et al. (1990), Eggleston et al. (1992), Mintz et al. (1994), Herrnkind et al. (1994), Butler et al. (1995), Lipcius et al. (1997), Butler and Herrnkind (1997), Herrnkind et al. (1997), Lipcius et al. (1998)	Marx and Herrnkind (1985)	–	Eggleston and Lipcius (1992), Mintz et al. (1994), Childress and Herrnkind (1997)
<i>P. marginatus</i>	Hawaii	–	–	Polovina and Mitchum (1994)	–	–	–
<i>J. edwardsii</i>	NZ	Butler et al. (1999)	–	–	–	–	Butler et al. (1999)
Clawed lobsters							
<i>H. americanus</i>	NE US, Canada	Lavalli and Barshaw (1986), Barshaw and Lavalli (1988), Wahle and Steneck (1992), Lawton and Lavalli (1995), Palma et al. (1999)	–	Fogarty and Idoine (1986), Wahle and Incze (1997), Peeke et al. (1998)	–	Castro and Angell (2001)	–
<i>H. gammarus</i>	Northern Europe	Van der Meeren (2000)	–	Howard (1981)	–	–	–
<i>N. norvegicus</i>	Northern Europe	Armstrong et al. (1991)	–	–	Bailey (1986)	–	–
Crabs							
<i>C. magister</i>	NW US, Canada	Fernandez et al. (1993b), Eggleston and Armstrong (1995)	Fernandez et al. (1993a,b), Armstrong et al. (1994), Fernandez (1999)	Fernandez et al. (1993a,b), Eggleston and Armstrong (1995)	Iribarne et al. (1994), Armstrong et al. (1994)	–	–
<i>C. pagurus</i>	North Europe	–	–	–	–	–	–

<i>C. sapidus</i>	East US, Gulf of Mexico	Pile et al. (1996), Eggleston et al. (1998b)	Hines and Ruiz (1995), Moksnes et al. (1997), Hovel and Lipcius (2001)	Eggleston et al. (1998b), Etherington and Eggleston (2000)	-	-	-
<i>C. maenas</i>	North Europe	Dumas and Witman (1993)	Moksnes et al. (1998)	Hedvall et al. (1998), Moksnes et al. (1998)	-	Goggin (1997)	-
<i>C. opilio</i>	E Canada, Alaska	Waiwood and Elner (1982), Bailey (1982), Robichaud et al. (1986, 1991), Lilly (1991)	Sainte-Marie et al. (1996), Lovrich and Sainte-Marie (1997), Dutil et al. (1997)	-	-	-	-
<i>C. bairdi</i>	Alaska	Jewett (1982), Livingston (1989)	-	-	-	Sparks (1982)	Stevens et al. (1994)
<i>P. camtschatica</i>	Alaska	Wespestad et al. (1994), Loher et al. (1998)	-	Loher et al. (1998)	-	Kuris et al. (1991), Tester and Mahoney (1995)	-

Table 5
Explicit references to density-dependent mortality, growth, or dispersal in the crab and lobster species surveyed in this review

Species	Location	Density-dependent processes		
		Mortality	Growth	Dispersal
Spiny lobsters				
<i>P. cygnus</i>	W Australia	Morgan et al. (1982), Ford et al. (1988), Phillips (1990), Caputi et al. (1995a,b,c)	Phillips (1990)	Phillips (1990)
<i>P. argus</i>	Florida, Bahamas, Belize	–	–	Forcucci et al. (1994), Butler et al. (1995), Herrnkind et al. (1997), Butler et al. (1997)
<i>P. marginatus</i>	Hawaii	Polovina (1989)	Polovina (1989)	–
<i>J. edwardsii</i>	NZ	Breen and Booth (1989)	Breen and Booth (1989), Pollock (1991)	–
Clawed lobsters				
<i>H. americanus</i>	NE US, Canada	Fogarty and Idoine (1986), Ennis and Fogarty (1997), Wahle et al. (2001)	Nelson et al. (1980), Wahle et al. (2001)	Wahle and Incze (1997), Incze et al. (1997)
<i>H. gammarus</i>	Northern Europe	–	–	–
<i>N. norvegicus</i>	Northern Europe	Hill and White (1990)	Bailey (1986), Pollock (1991), Hillis and Tully (1993a,b), Tuck et al. (1997)	–
Crabs				
<i>C. magister</i>	NW US, Canada	Fernandez et al. (1993a), Higgins et al. (1997), Iribarne et al. (1994), Botsford and Hobbs (1995), Botsford et al. (1998)	–	Iribarne et al. (1994), McMillan et al. (1995)
<i>C. pagurus</i>	North Europe	–	–	–
<i>C. sapidus</i>	East US, Gulf of Mexico	Hines and Ruiz (1995), Pile et al. (1996), Kahn et al. (1998), Uphoff (1998), Etherington et al. (2003)	–	Pile et al. (1996), Etherington and Eggleston (2000), Blackmon and Eggleston (2001), Etherington et al. (2003)
<i>C. maenas</i>	North Europe	Moksnes et al. (1998)	–	Moksnes and Wennhage (2001)
<i>C. opilio</i>	E Canada, Alaska	Sainte-Marie et al. (1996), Lovrich and Sainte-Marie (1997)	–	–
<i>C. bairdi</i>	Alaska	Zheng and Kruse (1999)	–	–
<i>P. camtschatica</i>	Alaska	Zheng et al. (1995)	–	–

over-compensatory juvenile-to-recruit relationships in these species. Cannibalism by older cohorts on younger ones can cause population cycling, a dominant feature of the dynamics of at least two of the crabs reviewed here: *C. magister* (Botsford, 1986; Botsford and Hobbs, 1995) and *C. opilio* (Sainte-Marie et al., 1996). In field experiments, habitat refuges, such as vegetation or crevices among shells, play an important role in mitigating post-settlement mortality by cannibalistic individuals (Fernandez et al., 1993a,b; Eggleston and Armstrong, 1995; Pile et al., 1996; Eggleston et al., 1998c; Moksnes et al., 1998; Etherington and Eggleston, 2000). These brachyurans feed opportunistically, and tend to be more fecund and settle at much higher densities than their lobster counterparts (Williams, 1984; Pollock, 1997), so it is perhaps not surprising that density effects are stronger and that cannibalism is a more important source of early mortality (Tables 1 and 3).

For most lobsters and crabs, the importance of predation to mortality is best viewed in the context of seabed habitat. There are numerous examples in which size-specific rates of survival have been related to the joint effects of habitat complexity and the type, size and abundance of predators, e.g., *C. sapidus* (Pile et al., 1996; Lipcius et al., 1998; Hovel and Lipcius, 2001), *H. americanus* (e.g. Lavalli and Barshaw, 1986; Barshaw and Lavalli, 1988; Wahle and Steneck, 1992), *P. argus* (e.g., Butler and Herrnkind, 1997), *Panulirus marginatus* (Parrish and Polovina, 1994). Settling in a protective habitat may bring temporary safety, but as juveniles grow they must emerge from the nurseries to satisfy demands for larger shelters or food. This brings renewed risks that can lead to heightened rates of mortality and a demographic bottleneck during emergence.

For lobsters and crabs that require the shelter of structurally complex habitats early in life, a demographic bottleneck may be defined as the heightened risk of mortality at an intermediate body size resulting from outgrowing available shelters before outgrowing the predation risk outside shelter (e.g., Wahle and Steneck, 1992; Wahle, 1992; Beck, 1995, 1997; Lipcius et al., 1998). The interaction of size-specific shelter availability and predation risk is illustrated in Fig. 2, which is an adaptation of a similar model described by Caddy and Stamatopoulos (1990). They modeled the mortality consequences of varying

size-specific shelter availability, but did not explore the effect of varying size-specific mortality outside shelter. Survival during emergence is determined not only by the size-specific probability of having shelter, but also by the size-specific probability of mortality without it (Fig. 2a). The bottleneck model predicts low survival for individuals that must leave shelter at a size still vulnerable to predation. Size-specific predation rates, however, are likely to vary in time and space. If predation rates are relaxed, emergent prey may experience high survival even if they have no shelter. This has important implications for recruitment because survival is not solely a function of shelter availability as the Caddy and Stamatopoulos (1990) model suggests. In some species shelter limitation at intermediate and large sizes may also have sublethal consequences such as inhibiting the moult, and thereby growth and egg production (Beck, 1995, 1997). Therefore, demographic bottlenecks at intermediate body size may be an important population regulatory mechanism in crevice dwellers such as lobsters and crabs.

There are fewer examples of food limitation on survival of crabs and lobsters. Nonetheless, there are numerous field reports of growth and body size being inversely density-dependent, mostly in lobsters (Bailey, 1986; Breen and Booth, 1989; Polovina, 1989; Phillips, 1990; Pollock, 1993; DeMartini et al., 1993; Hillis and Tully, 1993b; Tuck et al., 1997; Wahle et al., 2001). Food supply has been shown to influence habitat use in *P. argus* (Marx and Herrnkind, 1985) and *C. sapidus* (Mansour and Lipcius, 1991). To the extent cannibalism can be taken as evidence of food limitation, there may be many more examples among the crabs, although these studies have focused more on the mortality consequences than the growth effects of inter-cohort interactions (Tables 4 and 5).

Disease and other pathogens are still poorly understood as a source of post-settlement mortality influencing cohort success in large decapods. Reports of disease are infrequent (Table 4). Local mass mortalities of king crab (*P. camtschatica*) have been attributed to toxic algal blooms (Tester and Mahoney, 1995). Recently in southern New England, separate events of mass mortality and an outbreak of shell disease remain unexplained (Castro and Angell, 2001).

Social aggregations unrelated to mating are only observed among spiny lobsters (Table 4). Solitary as

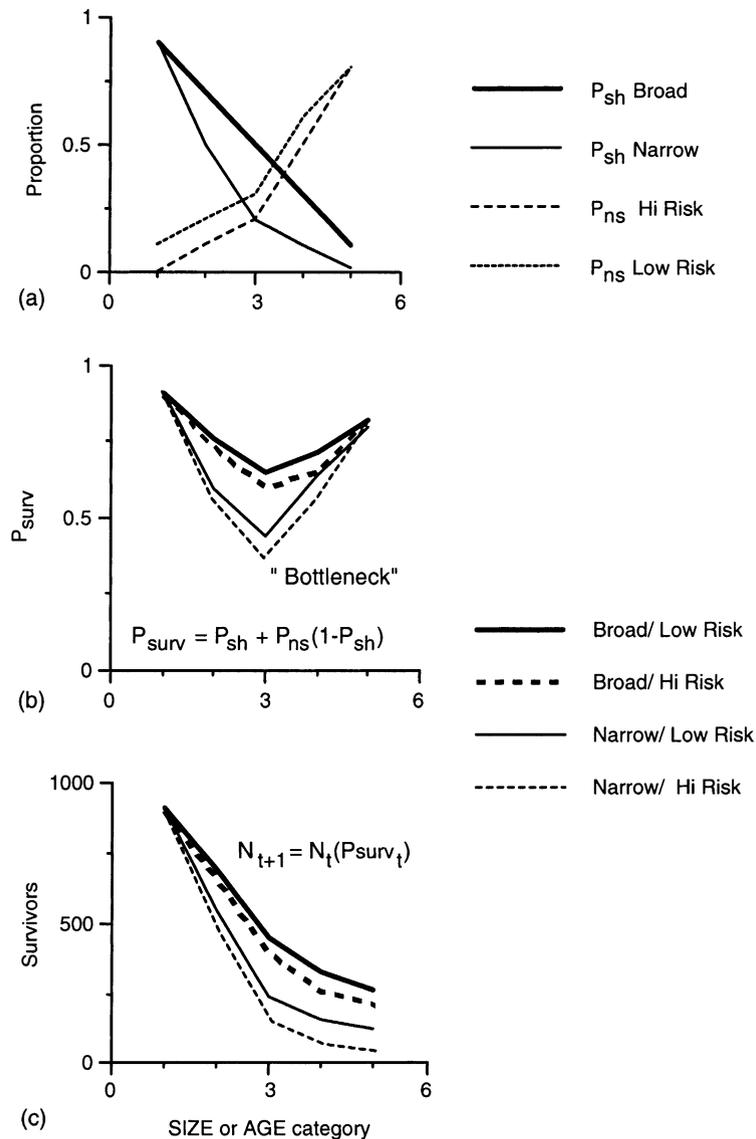


Fig. 2. Demographic bottleneck model describing the interaction between the size-specific probability of having shelter once settled and the probability of surviving without it. (a) In general, the breadth of available shelters (P_{sh}) will vary in space (and in time if biogenic). The probability of surviving without shelter (P_{ns}) may vary in space and time as predator diversity and abundance vary. (b) The probability of survival (P_{surv}) is a U-shaped function indicating the highest risk of mortality at an intermediate body size. The bottleneck may be more or less severe depending on size-specific shelter availability and mortality risk without shelter. (c) Survivorship starting with 1000 individuals under four scenarios of shelter availability and predation risk.

juveniles, they become increasingly social as they mature, and live in aggregations within the same shelter, a behavioral attribute that can both mitigate shelter limitation and deter predators (Table 4, Childress and Herrnkind, 1997; Butler et al., 1999). The only exam-

ple of a species with large mating aggregations among those reviewed is the tanner crab, *C. bairdii* (Stevens et al., 1994). The significance of social aggregations to the stock–recruitment function remains unclear, but may be an example of positive density-dependence if

sociality breaks down at extremely low levels of abundance (Allee, 1931; Myers et al., 1995).

Movements and migrations have been widely studied among crabs and lobsters. Seasonal patterns of activity, inshore offshore migrations, as well as counter-natant migrations by spawners, are well described in the literature for many of the species reviewed. Evaluating smaller scale movements during the early post-settlement stages has been more of a challenge though. Post-settlement dispersal may be an important means of mitigating crowding effects (Table 5, Pile et al., 1996; Incze et al., 1997; Etherington and Eggleston, 2000), but distinguishing post-settlement dispersal from mortality remains a challenge (Forcucci et al., 1994; Pile et al., 1996; Incze et al., 1997; Wahle and Incze, 1997; Butler et al., 1997; Moksnes and Wennhage, 2001; Etherington et al., 2003).

3. Case studies

3.1. Case 1: Western Rock lobster—*Panulirus cygnus*—supply dominated dynamics

The case studies begin with the western rock lobster, *P. cygnus*, because although the species is now largely managed on the basis of the recruitment forecasts from pre-settlement information (postlarval and oceanographic indices, Table 1), research conducted in the 1970s and early 1980s initially suggested stronger post-settlement density-dependent controls than are now recognized. The suggestion of strong density effects may have been due in part to a misinterpretation of experiments conducted at the time (Ford et al., 1988; Phillips, 1990). Losses to local reef populations, as evaluated from mark-recapture experiments, were initially taken to be mortality (Chittleborough and Phillips, 1975; Morgan et al., 1982). In retrospect, it became evident that some of the assumptions of the mark-recapture analysis were not satisfied and that the losses were more likely due to emigration (Phillips, 1990). This is an important lesson in experimental design because throughout the subsequent literature on post-settlement processes in crabs and lobsters researchers have been faced with the same challenge of distinguishing mortality from emigration losses. Surveys targeting only one habitat or a small area rela-

tive to the dispersal range of individuals can give misleading information if it is not recognized that individuals disperse or move to alternate habitats as they grow, so that declines in density do not necessarily mean declines in overall abundance (Incze et al., 1997; Etherington and Eggleston, 2000).

The demography of *P. cygnus* is now recognized to be largely driven by pre-settlement processes. The settlement index and oceanographic indices are sufficient to explain most of the variation in the catch at most locations (Caputi et al., 1995b,c). The catch of older juveniles or “whites” a year before harvest is used to refine postlarval (puerulus) index-based predictions. The postlarval-to-catch relationship is best described by a power function, indicating weak but detectable density-dependence over the intervening year. Little more has been published on the nature of density-related processes in *P. cygnus*.

3.2. Case 2: Blue Crab—*Callinectes sapidus*—post-settlement dominated dynamics

Of the decapods reviewed here, few have stronger evidence of the dominance of post-settlement processes than the blue crab, *C. sapidus*. A number of surveys and experimental manipulations reveal their strength and scope. Two lines of evidence present an instructive contrast to *P. cygnus*. First, there is evidence of strong compensatory and over-compensatory dynamics from stock–recruitment relationships (Table 1b). Second, over the past decade a number of important experimental approaches have been developed that elucidate the post-settlement processes influencing these relationships (Tables 2–5).

Blue crab life history contrasts with that of spiny lobsters in having a shorter larval life (weeks as opposed to months), with consequently far less dispersal potential (hundreds versus thousands of kilometers). Ovigerous females migrate downstream to the mouth of estuaries to hatch larvae. Larvae are exported to shelf waters and then reinvade estuarine waters where megalopae settle to shallow sea grass nurseries (Olmi et al., 1990; Johnson, 1995; Morgan et al., 1996). There is a much greater chance that larvae will recruit to the natal estuary because of the more restricted dispersal, thereby enhancing the possibility of a significant spawner-to-recruit relationship. Benthic juveniles, initially restricted to vegetated habitats, undergo

an ontogenetic habitat shift becoming more emergent and mobile with size (Pardieck et al., 1999).

Based on trawl surveys, significant spawner-to-recruit relationships have been documented in the Delaware (Kahn et al., 1998) and Chesapeake (Lipcius and Van Engle, 1990; Lipcius and Stockhausen, 2002) estuaries. Each case suggests strong density-dependent mortality during early benthic life. The potential for post-settlement density-dependent controls may be even stronger in Gulf of Mexico estuaries, although there is less direct evidence. Van Montfrans et al. (1995) noted that settlement was “up to a 100-fold greater for Gulf than Atlantic coast estuaries implying population limitation by post-settlement processes in the gulf and greater recruitment limitation in the Atlantic”, a conclusion later echoed by Guillory et al. (1998) in a review of Gulf of Mexico blue crab fisheries.

Numerous field experiments have been conducted with blue crabs to elucidate the nature of post-settlement processes. One approach has been to examine settler–recruit relationships on much finer temporal scales than is typically done by standard annual or semi-annual stock assessment surveys. For example, Pile et al. (1996) evaluated the relationships in density between first juvenile crab instar (J1) and subsequent stages (J2–9) from a 10-year time series of monthly or semimonthly suction samples at a single sea grass nursery site during the larval settlement period. Although strong compensatory relationships were observed, it was not possible to distinguish mortality losses from emigration, precluding inferences about cohort survival. Nonetheless, tethering experiments revealed higher predation rates on small juveniles in the open than in vegetated habitats up to the J8 stage. From the J9 stage onwards, survival was high regardless of habitat. While these results underscored the value of vegetated habitat to early survival in blue crabs, the question of the extent of post-settlement dispersion remained unresolved.

Subsequent multi-site monitoring of settlement in North Carolina lagoonal bays confirmed the importance of post-settlement dispersal through secondary planktonic resuspension, especially during storm events, to sites landward of initial settlement (Etherington and Eggleston, 2000). Whether post-settlement dispersal mitigates density-dependent

mortality during the early juvenile stages remains unclear (Blackmon and Eggleston, 2001).

Other field and laboratory experiments implicate cannibalism as an important source of post-settlement density-dependent mortality in blue crabs. Noting that young-of-year crab abundance was not a good predictor of 1-year-old abundance in trawl surveys, Hines and Ruiz (1995) carried out field tethering experiments in which 75–97% of the mortality was related to cannibalism on juveniles. Mortality of tethered crabs was lower in shallow than deeper waters, with greater body size in shallows suggesting refuges in space and size. Laboratory mesocosm experiments have provided more insight into the nature of blue crab cannibal–prey dynamics. For example, Moksnes et al. (1997) found that cannibalism began at the megalopa stage and that the effect of older age classes varied with size, habitat and predator density. Other mesocosm experiments with larger blue crabs indicated negative effects of high density on foraging activity (Mansour and Lipcius, 1991).

Effects of habitat structure in the landscape have been gaining greater attention in recent years and are proving to be complex for blue crabs. For example, sea grass patch size has different effects on early and late stage juvenile blue crab survival. Whereas Eggleston et al. (1998b) found that J1 crab recruitment was higher in large patches where predatory grass shrimp were rare, Hovel and Lipcius (2001) revealed an opposite effect: mortality rates of tethered juveniles was the greatest in larger patches where cannibalistic adults were more abundant. Contiguous tracts of sea grass can act as corridors for adult crab movement, thus determining the clam flats where they forage (Michaeli and Peterson, 1999). These examples demonstrated the value of large-scale multi-site and multi-scale field studies to our understanding of the mechanisms influencing the fate of cohorts and the interconnectedness of subpopulations after settlement. It will be important for future studies to disentangle the effects of habitat attributes such as area and connectivity to cohort survival.

3.3. Case 3: American lobster—*Homarus americanus*—supply or habitat limitation?

The question of recruitment versus habitat limitation has been controversial for the American lobster.

A strong influence on arguments in favor of compensatory dynamics grew out of a postlarval-to-recruit relationship analyzed by Fogarty and Idoine (1986) from a 20-year data time series gathered by Scarratt (1964). By assuming postlarval abundance could also be used as a proxy for spawner abundance, they inferred from this analysis that, because of strong compensatory effects, brood stock abundance would have to be reduced drastically before recruitment would be negatively impacted. Their conclusion was consistent with the relatively stable landings over previous decades in many regions (Drinkwater et al., 1996), as well as with behavioral studies on shelter competition and reports of the relative scarcity of nursery habitat (reviewed by Lawton and Lavalli, 1995). Notwithstanding the possibility that the Fogarty and Idoine (1986) analysis may not have satisfied the assumption of a closed population, their hypothesis was consistent with prevailing notions of habitat limitation for large decapods (Caddy, 1986; Caddy and Stamatopoulos, 1990).

Then, during the 1980s, a region-wide boom in lobster landings spread from the Canadian Maritimes through New England that continues in the eastern Gulf of Maine today (ASMFC, 2000; Steneck and Wilson, 2001). This cast more serious doubt on the notion of habitat limitation, supporting instead hypotheses that environmental forcing may play a stronger role in determining fishery recruitment than previously thought. However, an exhaustive analysis of correlations between temperature and subsequent harvests at appropriate time lags indicated that the boom could not be accounted for by temperature anomalies (Drinkwater et al., 1996). Other possible environmental correlates have not been comprehensively tested. During the 1990s, US National Marine Fisheries Service (NMFS) trawl surveys were also indicating a widespread increase in stock abundance and egg production (ASMFC, 2000). However, stock assessment models continued to warn, as they had for decades, that lobsters were overfished (ASMFC, 1996, 2000). It has become increasingly clear to fisheries scientists, managers and the industry that current stock assessment methods were inadequate to forecast trends in the harvest (Acheson and Steneck, 1997; ASMFC, 2000). Only recently has metapopulation modeling suggested that the resilience of intensively fished nearshore stocks may be due to larval subsidies from lightly exploited segments of the population off-

shore (Fogarty, 1998). Pelagic sampling and more recent modeling of larval transport are beginning to provide insight into the relative contribution of local and distant sources of recruits to American lobster populations (Harding et al., 1983; Incze and Naimie, 2000).

Meanwhile methods have been developed to fill gaps in our understanding of linkages between early and later life stages. In the absence of long time series, one strategy has been to evaluate linkages in space. For example, Miller (1997) related differences in lobster landings along the Nova Scotia coast to a consistent coast-wide pattern of postlarval abundance. Similarly, in the Gulf of Maine, regional differences in benthic juveniles correspond to the spatial pattern of landings (Steneck and Wilson, 2001), confirming long-standing patterns in the size composition of the catch in the northeast Gulf of Maine and Bay of Fundy (Huntsman, 1923).

If regional differences in the catch stemmed from long-standing differences in settlement, does it follow that it will be possible to forecast harvests from temporal fluctuations in settlement? Suction sampling methods have opened a window on quantitative relationships between larval supply and the abundance of juvenile lobsters from settlement to greater than the age of 3 years (Able et al., 1988; Wahle and Steneck, 1991; Incze and Wahle, 1991; Incze et al., 1997, 2000; Wahle and Incze, 1997). Forecasting to the harvest, however, remains a challenge because of the long time lag between settlement and the harvest (5–9 years), the absence of accurate aging tools and the poor understanding of variability in size at age. Thus, even though an American lobster settlement index has been maintained for more than a decade in New England (Wahle and Incze, 1997; Incze et al., 1997; Wahle, unpublished data), complete abundance projections are only available from 1998 onwards (Wahle, unpublished data), hardly long enough to put forecasts to a rigorous test against landings at this time.

The importance of post-settlement processes to the shape of any emerging settler-to-fishery recruit relationship for the American lobster remains to be seen. It will be important to assess mortality associated with density-independent and density-dependent processes. Field experiments have been helpful in this regard. Small lobsters are vulnerable to predation outside the safety of shelter-providing habitats like cobbles and boulders and the association with shelter relaxes with

size (Lavalli and Barshaw, 1986; Wahle and Steneck, 1992; Wahle, 1992). Cannibalism has not been observed in nature in the American lobster, although it has in captivity, underscoring the need to take care in drawing conclusions from laboratory experiments alone.

As for density-dependence, field studies that combine long-term sampling, habitat manipulation and 'saturation' seeding experiments suggest that larval supplies are rarely sufficient to saturate available shelters at the time of settlement and that survival rates are high while lobsters are in the cryptic phase. As cohorts age, however, shelter availability is more likely to be at a premium and lobsters must move to alternative sites (Wahle and Incze, 1997; Incze et al., 1997, 2000; Palma et al., 1999). This may represent a demographic bottleneck (Fig. 2) for the American lobster in this region, but the mortality consequences of emergence remain difficult to quantify. It is possible that this may be a critical stage at which recruitment to the fishery is regulated. On the other hand, if mortality risks at the time of emergence are low, the bottleneck may be weak leading to a more linear relationships between settlement and recruitment than might have been conceived by Fogarty and Idoine (1986).

It is possible that mortality risks to emergent American lobsters have relaxed over the past two decades, as many commercially exploited ground fish have been depleted in the Gulf of Maine (Witman and Sebens, 1992; Jackson et al., 2001). If that is true, it is also possible that mortality during density-related dispersal from nursery habitats may be lower than at earlier times when predators were larger and more abundant. It is, therefore, as important in the case of the American lobster as it was in the previous two cases to design studies that differentiate mortality and emigration. In the meantime the jury is still out as to whether changes in predation or some other environmental factor(s) may be linked to the recent surge in American lobster abundance.

4. Conclusions and future research

The rarity of significant spawner-to-recruit relationships in crabs and lobsters is likely a result of the vagaries of the pelagic environment and its influence on larval supply and survival before juveniles recruit

to the benthos. There are more examples in which environmental indicators of the strength of transport processes, either with or without spawner abundance, predict recruitment strength better than spawner abundance alone. It follows that we should find even more examples of significant juvenile-to-recruit relationships, because the benthic recruits have already passed through the filter of the pelagic environment. The few examples of significant spawner-to-recruit relationships have occurred where the spawner population has either been depleted enough to overwhelm the environmental noise (e.g., *P. cygnus*, Caputi et al., 1995a), or where a relatively tight linkage has existed in space and time between larval hatch and recruitment to subsequent benthic stages (e.g., *C. sapidus*, Lipcius and Stockhausen, 2002), more typical of relatively short-lived caridean shrimp (Cobb and Caddy, 1989).

Post-settlement density-dependence seems to be more the rule than the exception among the taxa surveyed. For virtually all the species in which juvenile-to-fishery recruit relationships have been documented, non-linear relationships provide the best statistical fit. These range from power functions for the species with the weakest density effects, such as *P. cygnus*, to Ricker functions among the species, such as *C. sapidus*, for which fecundity, larval retention and settlement is high, and for which there is evidence of strong density-dependent post-settlement cannibalism. Still, there are a number of commercially exploited species for which we have little information on stock–recruitment relationships.

Field experiments have provided direct evidence of the relative importance of pre- and post-settlement processes to recruitment, and nature and strength of post-settlement density-related mechanisms. Except for quasi-closed populations such as blue crabs in large estuaries, spatial patterns of settlement in most of the lobsters and crabs reported here relate to larval transport processes far more often than they relate to the location of the parent stock. Post-settlement survival is strongly influenced by the three-way interaction of predation risk, habitat quality and body size. As a result, refuge habitat is more often a limiting factor than food, especially among small individuals still vulnerable to predators. That is why it is necessary to understand the nature of demographic bottlenecks in terms of the joint effect of habitat availability

and critical predator–prey interactions. Some of the most recent work on habitat effects are going beyond small-scale structural complexity and are beginning to assess landscape scale effects such as patch area, inter-patch distance and connectivity. Early findings suggest that it is not valid to simply scale up mortality rates observed in small-scale experiments.

Experimental interventions have provided useful insights into post-settlement processes, but they are not a panacea. This is especially true where estimates of mortality are confounded by dispersal-related losses. Post-settlement movements create special challenges for the study of large-bodied benthic decapods that set them apart from more experimentally tractable sessile or sedentary species. Benthic movements may occur almost immediately after settlement while still in the postlarval stage or after an initially sedentary and cryptic early benthic phase. Dispersal may mitigate crowding effects in many species and, thus, can affect a population's distribution but not its abundance. It will be important to design future surveys and experiments in a way to differentiate emigration and mortality in open populations of crabs and lobsters.

Difficulty in the interpretation of spawner- or juvenile-to-recruit relationships has stemmed from a poor understanding of larval subsidies to, or post-settlement emigration from, the study area (e.g., Fogarty and Idoine, 1986; Phillips, 1990; Pile et al., 1996; Ennis and Fogarty, 1997). It is important to recognize that in open populations: (1) larval supply is independent of the local spawners; (2) declining benthic densities do not necessarily translate to declining abundance, if individuals have moved to areas or habitats outside the scope of sampling. The consequence can be to misinterpret a recruitment-limited population as a habitat-limited one. Fogarty's (1998) metapopulation analysis represents one of the first examples in which spatially linked subpopulations have been incorporated into a yield model with important implications regarding the resilience of stocks to harvesting.

Cannibalism appears to be exclusively seen in crabs, although not in all species. Cannibalism is an important density-dependent contributor to post-settlement mortality. Inter-cohort cannibalism may explain cycles in the abundance of Dungeness (*C. magister*) and snow crab (*C. opilio*). Spiny lobsters are the only group sur-

veyed here that forms social aggregations for reasons other than mating. Spiny lobsters become social after their early cryptic juvenile stage and sociality may mitigate crowding as they grow. Experimental work has demonstrated clear survival advantages of living in groups (Childress and Herrnkind, 1997; Butler et al., 1999).

Age determination remains a challenge unique to crustaceans and continues to frustrate efforts to follow cohorts through a population. Sheehy (2001) recently pointed out the spread in size with age can be another contributor to stock–recruit relationships being misinterpreted as compensatory. Continuing developments in the use of “age pigments” and tagging Bannister et al. (1994) may shed some light on this perplexing problem. In addition to those discussed above, there are several other emerging areas of research that will contribute to our understanding of post-settlement processes influencing recruitment. One such area is the study of depensatory processes, such as the function of social aggregations (Butler et al., 1999), and the influence of sperm limitation in populations where males are selectively harvested. Disease and pathology is another area in which the consequences to survival and recruitment are poorly understood and may be either episodic or closely coupled to population density (Castro and Angell, 2001).

Over the past decade or so, a combination of monitoring and experimentation has led to major strides in our understanding of recruitment processes for certain well studied species, mostly in North America, Australia and New Zealand. Essential demographic information is lacking, particularly of early life stages, for commercially important European species such as *Homarus gammarus*, *Nephrops norvegicus* and *Cancer pagurus*. Finally, in answer to the question posed in the title of this paper, experimental ecology may be best viewed as one of the keys in a three-part strategy proving to be most productive in ecological assessment and forecasting (Bjornstad and Grenfell, 2001; Brown et al., 2001; Clark et al., 2001): (1) *modeling* as a means to put testable hypotheses in a larger dynamic framework; (2) long-term and comprehensive *monitoring* as an indispensable means of documenting changes and linkages in distribution and abundance of different segments of the life history, and as a means of ground-truthing model predictions; (3) *experimental interventions* conducted at times and

spatial scales appropriate to specific hypotheses and model predictions.

Acknowledgements

Support during the preparation of this review was provided in part by NOAA/Sea Grant. Thanks go to the organisers of these meetings for their invitation to contribute this paper and for travel support. Assistance with the literature search was provided by S. Kirby and N. Sosin. The manuscript was improved through illuminating discussions with M. Fogarty, L. Incze, R. Lipcius, and R. Steneck, and by thoughtful comments on earlier drafts by M. Dunnington, K. O'Donnell and two anonymous reviewers.

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